

EFFECT OF HIGH TEMPERATURE ON FRUIT SET OF SELECTED GENOTYPES OF
LYCOPERSICON ESCULENTUM MILL.

A Thesis
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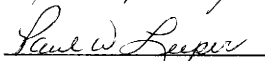
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ABSTRACT

Effect of High Temperature on Fruit Set of Selected Genotypes of

Lycopersicon esculentum Mill. (December 1982)

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High temperature effect on style length, pollen viability and embryo sac viability were studied in 5 tomato genotypes ('9', '110', '200', '229' and 'FD'). Plants were grown under 2 different temperature regimes at Weslaco, Texas and were compared for fruit set: 1) Summer of 1980 (avg. max. temp. 37.1°C ; highest max. temp. 39.9°C), 2) Summer of 1981 (avg. max. 33.1°C ; highest max. temp. 35.6°C). Fruit cross sections showed that all 5 genotypes produced fruit (from red ripe to small green) containing seeds and gel from plants that developed over a 50 day average maximum temperature of 33.1°C ; plants that developed over a 50 day average maximum of 37.1°C resulted in no fruit production on plants of genotype 'FD' and parthenocarpic fruit for genotypes '200' and '229'. Genotypes '9' and '110' produced seeded mature fruit at the high temperature, while some locules of small green fruits lacked seeds and gel at high temperature.

For the embryo sac viability study, flowers used for comparison developed under the following temperatures: 1) flowers collected on May 1 or 20, 1981 in College Station with the average maximum temperature over 14 days prior to the collection of 27.2°C and a highest maxi-

mum of 32.2°C, 2) flowers collected on July 16, 1980 at Weslaco with the average maximum temperature over 14 days prior to collection of 36.9°C and a highest maximum of 37.8°C. Microscopic observations of embryo sacs observed in slide sections revealed a large percentage of high temperature flowers (avg. max. 36.9°C) of all genotypes studied contained degenerated embryo sacs, 'FD' containing the most and '110' the fewest degenerated. From the flowers collected at favorable temperature (avg. max. 27.2°C), few degenerated embryo sacs were observed for any of the genotypes.

Style length increased with increasing temperature for all 5 genotypes, but at the highest temperature, only genotype '110' had inserted styles in all flowers sampled. Pollen viability decreased sharply with increasing flower development temperature > 30.6°C for all genotypes except '110' and '200'. Pollen germination of genotype '110' remained high (as great as 56% germination) over the entire temperature range studied.

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INTRODUCTION

Tomato fruit set at high temperature has been widely studied over the years, and various authors have attributed failure of set to stylar elongation, degeneration of embryo sacs, pollen sterility, decreased pollen production, and slow pollen tube growth (35). Johnson and Hall reported that the most critical factors contributing to low tomato yields in Texas during summer are unfavorably high temperature and light intensity, which prevails from June through September (27).

In East Texas, tomatoes require blooming season temperatures of 21.1-30°C day/15-20.6°C night for at least 36 days in both April and May to set large crops of fruit. They usually set few or no fruits when temperatures are warmer from June to August (74). Favorable temperatures were most beneficial over periods of 3-10 consecutive days (72). The fruit of most varieties tends to become smaller during the hot, dry summer period. For example, the normal fruit weight of 'Bonny Best' is 125-155 grams while the average weight for this same variety at College Station at the end of August in 1937 under unfavorable high summer temperature was only 24.7 grams (20).

In the first large scale hybrid seed production tests conducted at Auburn, Alabama in 1939, it was observed that pollinations made on certain days resulted in a relatively high percentage of fruit set, whereas on other days a very poor set was obtained. In general, the hotter and dryer the day, the poorer the results (3).

This thesis follows the style of the Journal of the American Society for Horticultural Science.

Went concluded that night temperature is more important than day temperature for fruit set, and fruit is set abundantly only when night temperatures are between 15 and 20°C with the optimum being 17-19°C (66). Young reported that the favorable temperature range for tomato fruit set is 21.1-29.4°C day/12.8-20.6°C night (72, 73). Charles and Harris reported that the highest percentage fruit set in selected genotypes occurred at 18.3°C as compared to 12.8 or 26.7°C, and larger fruit was produced at 18.3°C (7).

The temperature range within which most tomato varieties produce commercially profitable amounts of fruit is surprisingly narrow and one or two degrees difference in night temperature may mean production of only half or one-third the potential yield (67). In contrast, humidity, length of photoperiod, light intensity, mineral nutrition, root temperature, watering, and root media could be varied within wide limits without significantly changing the rate of stem elongation or fruit set (66).

The objective of this study was to select several genotypes with diverse phenotypic expression at high temperature for use in studies to determine temperature effects on style length and temperature effects on pollen and embryo sac viability--factors which are believed to be responsible for failure of tomato plants to set fruit during hot, Texas summers.

LITERATURE REVIEW

Flower Anatomy and Embryology

Cooper (8, 9) described the tomato flower and inflorescence from studies of the cultivars 'Bonny Best' and 'Greater Baltimore'. The flower cluster of the tomato is a short, forked racemose cyme of seven to twelve flowers. It is unusual for more than two flowers to open at one time in each inflorescence, so that a peduncle is often found bearing small fruits, open flowers, and developing buds at the same time. The tomato flower is perfect, hypogynous, regular, pendant, and typically six-merous (8). The ovaries in the varieties studied by Cooper consist of six united carpels with an enlarged placenta on the inner or axillary wall of each carpel on which the ovules are borne. Development of the ovule of the tomato conforms to the type found in most of the Sympetalae (9). The six or more orange-yellow stamens are attached adnatly to the throat of the corolla tube, and are connivent or syngenesious and form a cone around the stigma (8, 12).

Anther and Microspore Development

Each anther is divided longitudinally into a right and left lobe, separated by the connective tissue. Each lobe contains two microsporangia which extend approximately the full length of the anther. After the development of spore mother cells from the sporogenous cells, the conjunctive or sterile tissue separating the sporangia of each lobe breaks down, leaving one spore chamber (pollen sac)

in each lobe (8).

The tapetum is a single layer of cells that lines the microsporangial cavity and serves as a nutritive layer for the developing pollen mother-cells and subsequently developed microspores. At anthesis, nothing of the tapetal cells remains but a thread-like vestige in the periphery of the cavity. Degeneration of the tapetum starts at various times, but is generally evident by the time of the first and second meiotic metaphases in the pollen mother cells (46).

After the uninucleate microspores are released from the old pollen-mother cell wall, they quickly assume a spherical shape and enlarge until each finally reaches a volume comparable to that of the original pollen mother cells (46). Pollen grains are almost mature at the 4-celled embryo sac stage. At this time they are 2-nucleate, containing a spherical generative nucleus and a spherical vegetative nucleus. The generative nucleus again divides within the pollen tube before reaching the embryo sac (57).

The endothecium--the outermost layer of the anther wall nearest the junction of the two microsporangia of an anther lobe--develops in a special manner so as to serve as the disjunctive layer. Timing of the final stages of development including anthesis of the flower can be followed accurately in the differentiation of those endothelial cells that regulate the opening of the dehiscence slit. In the final stages these cells elongate radially and they retain an active condition longer than any other sterile cells of the anther (46). The splitting is introrse, so that the pollen grains fall on the stigmatic surface of the pistil. The papillae of the stigmatic

surface secrete a sticky fluid in preparation for pollination (8).

Ovule and Embryo Sac Development

About the time when the single integument is beginning to develop, a hypodermal cell of the nucellus is differentiated as the archesporial cell. The archesporial cell does not divide to form a primary parietal and a primary sporogenous cell, but functions directly as a megaspore mother cell. As the megaspore mother cell enlarges, it is surrounded at its apex and sides by a unicellular layer, and its base is embedded in the nucellus. The integument begins as a meristematic outgrowth surrounding the ovule at a level just below that of the archesporial cell and grows outward around the apical portion of the nucellus. At the time when cell division is completed following the meiotic I division, the developing integument has almost surrounded the nucellus, and it has formed a micropyle of some length by the time the four megaspores are formed. Cell division in the integument is in many planes, so that it grows in thickness as well as in length. A linear row of four megaspores is produced. The megaspore at the chalazal end of this row functions as the embryo-sac, the other three spores disintegrating. The inner layer of the integument, which is now in contact with the embryo sac, is differentiated as a nutritive layer (9).

At the time when the microspore mother cells are in early prophase, the ovules appear as erect, rounded protuberances arising from the placental tissue. These protuberances soon become somewhat pointed, and growth is more rapid on one side of this mass of cells

than on the other. As a result, each ovule becomes anatropous (9).

When the microgametophyte is in the telophase of the second division, the megagametophyte is in the hypodermal-archesporial-cell stage (57). Lesley discovered that the megaspore mother cells are in the prophase stages of the first reduction division when the pollen mother cells are in stages of cytokinesis (34). When the megaspore mother cell is in the metaphase I stage, the collar-like integument has reached the level of the apex of the ovule. Young microspores are to be found in the anther sacs at this stage of ovule development (9).

Ovule Development. Rick (45) described the appearance of fertile and sterile ovules at anthesis. A fertile tomato ovule contains an embryo sac that is highly vacuolate and greatly distended. The embryo sac is broadly ellipsoidal, its dimensions in these preparations averaging $41 \times 63 \mu$. The same features are found in freehand sections of living ovules. Since the nuclei of the embryo sac are distributed in various planes throughout this large cavity, it is seldom possible to find all nuclei in a single microtome section. Despite this enlarged condition, one can readily identify normal embryo sacs by scanning serial sections.

The synergid cells are characteristically cuneate in shape. At anthesis the nucleus appears at the narrow micropylar end of the synergid cell, while a single vacuole occupies the other broadened end. The egg cell is usually in contact with the synergids, often surmounting their vacuolate ends. The polar nuclei, which at anthesis may exist in separate or fused condition, usually appear midway

between the micropylar and chalazal ends of the embryo sac and are found mostly in the peripheral cytoplasmic layer. Occasionally, however they may be observed in the center of the large vacuole, connected with the periphery by thin cytoplasmic strands. The three antipodal cells disintegrate during the later stages of maturation: as a rule, only vestiges of them remain at anthesis. The nucellar epidermis, which collapses earlier in development, is recognized at anthesis only by a thin layer of crushed cell walls immediately surrounding the embryo sac. The remains of the nucellar epidermis are surrounded by densely cytoplasmic parenchymatous, integumentary cells, roughly isodiametric in shape. The main body of the ovule consists of similar, though more vacuolate cells. The single integument is penetrated by a micropyle, whose length averages $125\ \mu$ (45).

Gamete Viability

Levy reported that the functionality of both types of gametes was reduced by high temperature as expressed by reduced rate of fruit set but that microspores were more affected than megaspores (35). Shelby reported that heat sterility at 30°C was due to insufficient pollination and reduced pollen tube growth but that no significant loss in embryo sac viability occurred at temperatures as high as 33°C (55). In contrast, El Ahmadi discovered that based on fruit set, ovules were affected by high temperature more drastically than was pollen. Seed set indicated that ovule viability was reduced by high temperature in all cultivars tested (14).

Stages of Susceptibility to Heat Treatment

Iwahori and Takahashi conducted experiments to determine at what stage flower buds are susceptible to high temperature damage. Iwahori exposed tomato plants bearing flowers at various stages of development to 40°C for 3 hours on 2 consecutive days and found that the buds most affected were those 9 to 5 days before anthesis and 1 to 3 days after anthesis. The number of days to anthesis was determined by correlating bud lengths of treated flowers to previously determined bud stage lengths. The result of the heat treatment at various numbers of days relative to anthesis were: 11 days before anthesis, 100% set; 9 to 5 days before anthesis, 10 to 20% set; 3 days before anthesis, 70% set; 1 day before anthesis, 100% set; 1 to 3 days after anthesis, 10 to 20% set; 8 days after anthesis, 100% set (23). Iwahori concluded that the meiotic stages of bud development are most susceptible to high temperature damage. He determined that meiosis occurs in microspore mother cells 9 days prior to anthesis and at 8 days before anthesis in megaspore mother cells. In plants treated 9 to 7 days before anthesis, pollen tetrads became degenerated and megaspores also were degenerated or developmental stages delayed. High temperature treatment 4 to 6 days before anthesis resulted in 20 to 50% empty pollen grains while the egg cells and polar nuclei were degenerated (24).

Rudich confirmed Iwahori's findings that the meiotic stage is most susceptible to heat damage after giving plants 1 treatment of 4 hours at 40°C and finding that the most damage occurred to gametes when plants were treated at 9 days before anthesis. When 'RomaVF'

plants were heat treated 9 days before anthesis, the reduction in percent fruit set was more pronounced than the reduction in pollen viability (50). Sugiyama et al. heat treated plants at different stages according to leaf number and followed the effects throughout the plants' development. Plants were exposed to temperatures of 35⁰, 40⁰, and 45⁰C for 3 hours/day on 5 successive days. Positions of flowers in each cluster were mapped at the time of heat treatment and fruit set was recorded for those flowers and for clusters that developed after treatment. It was found that in plants treated at the first cluster stage, effects on the second and third cluster stage diminished so that percent set increased with time from treatment (58). Kuo performed similar treatments with chinese cabbage by heat-treating at 34-37⁰C at different growth stages for 3 days. The bud stages most susceptible to heat treatment was found to be 1-3 days before and after anthesis (30).

Embryo Sac Degeneration in Other Species

Ormrod et al. studied the effect of temperature on embryo sac development in Phaseolus vulgaris L. and reported that very few embryo sacs with degenerated contents were found at 24/15.5⁰C and 29.5/21⁰C, but the proportion of these increased strikingly with time at 35/26.5⁰C. Although development appeared normal at 24 hours prior to anthesis in flowers grown in 35/26.5⁰C almost no embryo sacs developed endosperm at this temperature, and a large proportion of the embryo sacs had degenerated contents within 48 hours after anthesis. It was concluded that the almost complete lack of fruit

set found in Phaseolus vulgaris L. at 35/26.5°C can be related to the degeneration of the contents of the embryo sac beginning approximately at anthesis (42).

Protogynous flowers of avocado were collected at anthesis, sectioned, and observed for ovule degeneration. The avocado embryo sac is of the polygonum type. Degeneration of the ovule occurred in the embryo sac. Apart from the antipodals, degeneration concerned mainly the egg apparatus and, less frequently, the polar nucleus. One, 2 or all 3 cells of the egg apparatus may degenerate. Five grades of degeneration were distinguished and described. All stages are accompanied by more or less drastic discoloration. Instead of the well-defined, bright, differential staining of the intact egg apparatus, a blotch of mixed colors marks the degenerate one (61). In the majority of degenerate ovules a degenerate egg apparatus was seen, and the filiform apparatus proved to be the most stable part of it, still recognizable when all other parts were no longer identifiable (62).

Examination of the flower buds at different stages revealed that degeneration of the avocado embryo sac at the micropylar site may occur at the four-nucleate stage or at egg-apparatus organization, prior to or after the filiform apparatus has formed. The time of occurrence of degeneration decisively determines the appearance of the degenerate remnants (62).

Pollen Production, Dehiscence, and Viability

Abdalla and Verkerk reported that far more pollen is produced

at normal than at high temperature (1). El Ahmadi reported that all varieties tested (including the heat tolerant 'Saladette') showed extreme reduction in pollen produced at high temperature as measured by pollen weight per flower, and at high temperature, the majority of flowers did not release any pollen. El Ahmadi concluded that this extreme reduction (71 to 96%) in pollen weight was probably largely due to indehiscence (14).

Shortly after anthesis the pollen is released from the anther thecae through lateral slits or stomia. The pollen is then largely confined to chambers, each bounded by the walls of adjacent thecae of two cojoined anthers. From this position the pollen finds its way into the central chamber surrounding the style largely through openings near the terminal sterile tips of the anther. From the central chamber the pollen drifts toward the distal opening of the tube, this end of the tube usually being lower in the natural position of the flower. As it passes, some of the pollen is deposited on the stigma, which usually appears at the mouth of the tube or slightly within it (47).

Levy reported that high temperatures during development of the heat sensitive cultivar 'Hosen Eilon' strongly affected quantity of pollen, its viability, and growth rate of pollen tubes cultured at 25°C (35). Rudich discovered that endothecium thickening failed to occur in the heat sensitive cultivar 'Roma' while it formed normally in the heat tolerant cultivar 'Saladette'. The endothecium is essential to stamen and pollen theca opening (50).

Howlett reported that in flowers and plants suffering from severe carbohydrate deficiency, degeneration of the anthers occurred before the development of a distinct sporogenous tissue. Under conditions of less severe carbohydrate deficiency, many pollen grains were developed which were morphologically perfect, which took the aceto-carmin or rethnium red stains deeply, but which failed to germinate on the stigma or the agar media. Howlett concluded that microspore degeneration and pollen sterility correlated positively with the degree of carbohydrate deficiency (21). Johnson and Hall compared carbohydrate content of 'V617 Pearson' which failed to set with that of 'S-1119' which fruited vigorously in summer and found that in neither case were carbohydrates low enough to be limiting set (26).

Pollen Germination

"In Vitro". Pollen germinability may be assessed by in vitro germination counts or in vivo tube growth in sectioned styles or by seed formation in developing fruits. Charles and Harris (7), El Ahmadi (14), Abdalla and Verkerk (1), and Levy (35) all performed in vitro pollen germination tests. Abdalla and Verkerk (1) and El Ahmadi (14) used a medium solution of 5% sucrose in 100 ppm boric acid. Charles and Harris (7) did not list their media contents. Levy (35) used a medium devised by Brewbaker and Kwack containing 10% sucrose, 100 ppm H_3BO_3 , 300 ppm $Ca(NO_3)_2 \cdot 4H_2O$, 200 ppm $MgSO_4 \cdot 7H_2O$, and 200 ppm KNO_3 (5). El Ahmadi scored pollen grains after 4 hours on media (14). Smith reported the optimum temperature to be $29.4^{\circ}C$

for germination and 21.1°C for tube growth, although little difference existed between 21.1 and 29.4°C for germination (57). Abdalla and Verkerk reported the optimum temperature for germination and tube growth to be 27°C and that germination is evident after 2 hours. At 42°C , they detected no germination, only shrunken and ruptured pollen grains, but they concluded that pollen produced at high temperature will germinate, but tube growth is slower (1).

"In Vivo". Charles and Harris (7) observed in vivo pollen germination using excised styles stained with aniline blue and exposed to UV light to create fluorescent pollen tube bands according to the methods of Martin (38). Charles and Harris also found that pollen from plants grown at 18.3 or 26.7°C produced tubes that penetrate the ovary in 24 hours when cultured in plants at 18.3 or 26.7°C , but the pollen took 84 hours to penetrate when cultured at 10°C (7).

Twelve hours was found to be long enough for the pollen tube to pass through the style in most cases when the stigma was mature when pollinated (17). The pollen, after being deposited on the stigma, remains inactive for several hours. At 6 hours after pollination at 21.1°C and 29.4°C numerous short pollen tubes had entered the tissue of the stylar canal growing between the cells. At 37.8°C , however, only 0.1 percent of the pollen grains had germinated during the first twelve hours after pollination. The pollen tubes at this temperature were extremely short. The maximum percentage germination (6.3%) at 37.8°C occurred 42 hours after pollination (57).

Abdalla and Verkerk performed controlled pollinations using pollen and pistillate plants grown at high temperature (35° day/ 25°

night) or normal temperature (22° day/ 18° night) and found that 7 of 10 high temperature pollen crosses showed no tubes in normal temperature flowers, and the tubes that were produced failed to reach the ovaries after 48 hours. Normal temperature pollen X high temperature flowers gave better set (1). El Ahmadi performed controlled pollinations at the onset of night temperature which was more favorable for pollen germination and tube growth than day temperature (14).

Pollen germination and rate of pollen tube growth were measured in all treatments by collecting 2 styles from each of the crosses at 6, 9, and 12 hours after pollination, and observing pollen tube fluorescence by Martin's technique. Both pollen tube growth and pollen germination were greatly reduced during the midnight-6 A.M. period. Temperatures in the field on the day of treatment were high- 32.8°C , low- 10°C . Pollen tubes were able to grow to the base of the style in 6 hours during the day and evening; 12 hours were required during the early morning hours (13).

Flower Stages and Anthesis

Smith noted that corollas remained open and stigmas were receptive for an average of four days. The anthers normally dehisced at the beginning of the second day of anthesis (57). When the corolla begins to open the stamens are of a greenish-yellow color, and the pollen sacs are completely closed (17). After 24 to 48 hours, depending on atmospheric conditions, the color of the stamens changes to a bright yellow and dehiscence begins (8, 17). The average time required for sacs to begin to open after the corolla has started to

expand is two days, but there is a considerable amount of variation in the time due to the size of the flower and to the hygrometric state of the atmosphere. The pollen sacs open sooner in dry than in wet weather (17).

Scott and George (54) described the stages of flower development at pollination:

1. Early--sepals beginning to reflex, petals white and not reflexed, anthers green, 3 days before anthesis.
2. Mid--sepals and petals reflexed $45-90^{\circ}$, petals and anthers greenish-yellow, about 1-2 days before anthesis.
3. Late--sepals and petals reflexed 90° , petals and anthers bright yellow, at anthesis.

Pollen is obtained from any flowers having their petals well reflexed, turned back, or fully expanded, in which stage of development the anthers are dehiscent or freely discharge pollen. The stigma is in a receptive condition at the time the petals first close after having been previously reflexed. Later on the petals close together, fade in color, and begin to shrivel and dry. After several days they will often dry quite hard and stiff, remaining persistent to the calyx for a short period before dropping (4). Emasculation must be carried out before the petals are fully reflexed, as the anthers begin to dehisce before that stage is reached (3).

Pollination becomes most effective when petals are fully reflexed. A 12.5% set was secured by pollinating at calyx and corolla opening. When the calyx and corolla were open but not reflexed, a 64.3% set by pollination (49). When flowers just opening were

emasculated and their pollen used to pollinate other emasculated flowers, the pollen grains were not effective. When the emasculated flowers were pollinated with mature pollen, fruit was produced (17).

Flowers were emasculated as much as 24 hours before pollen ripened. A test was made to determine whether the stigma was in a receptive condition at that time. When pollinated immediately, 76% of the blossoms set fruit, but a set of only 57% was obtained when pollination was delayed until the following day. Even poorer results were obtained when pollination was delayed 2 or 3 days. The period of receptivity of the stigma may be a varietal characteristic (3).

The length of time that the stigma is in such condition that pollen placed on it will fertilize the egg, it was found to be from four to eight days, and during the first day or two the flowers cannot be close-pollinated as the pollen sacs are not yet open (17).

Fertilization

Fertilization was first seen 50 hours after pollination and the zygote appeared fully formed several hours later. After fertilization the zygote does not begin division for 36 to 48 hours. It was not until 94 hours after pollination, or 44 hours after fertilization that the first two-celled embryos were found. The primary endosperm nucleus begins division in advance of the embryo. At 66 hours after pollination, when the embryo is still one-celled, the endosperm consisted of eight cells with definite walls separating them (57).

Cross Pollination

The number of seeds per fruit resulting from cross pollination was relatively small compared with the average number observed in normally pollinated fruits of the same variety (3). Shelby et al. concluded that at high temperature, both heat sensitive and heat tolerant cultivars did not give maximum fruit set by self-pollination (55). Rudich also concluded that artificial pollination greatly increased percent fruit set in all cultivars studied (50).

Fruit Set

Physiology of Fruit Set and Flower Drop

Flower drop during hot weather often occurs due to lack of fertilization (35). Failure of tomato flowers to set fruit is usually expressed in one of two ways: either flowers abscise from the plant or sepals enlarge and the flower remains attached to the plant with the tiny ovary in a static condition (33). Johnson and Hall reported that tomatoes having a raceme type inflorescence do not abscise but rather the ovary remains in a dormant condition until favorable environmental conditions for set (26). Radspinner noted that drop may occur at any stage of the blossom but seldom after the fruit has set, and it occurs only during periods when the air is extremely hot and the relative humidity low (44).

Over a two-week period up to five pollinations were made on each flower cluster and the set of fruit was later recorded. A good set of fruit was obtained on the first, second, and third flower to

open on each cluster. A sharp drop was noted with the fourth flower and only a small percentage of the fifth flowers resulted in a fruit (3). It is usually the flowers farthest from the base of the cluster that stop growing for a time or abort. The fruits nearer the base begin to grow first and take most of the nourishment till full grown. Some ovaries become aborted at about one-fourth the size of a pea, but hang on the vines for a month or two (17). A common difficulty in the growing of a winter crop of tomatoes in the greenhouse is the failure to secure a satisfactory set of fruits on the lower clusters. This is particularly true if the plants are grown with sufficient vigor to insure a set of fruit on the upper clusters. The lower blossoms persist and are often referred to as "vegetative blossoms" (49). Percent fruit set is under the control of a largely additive system with a moderate heritability at high temperature (15).

Leopold and Scott attempted to discover why undeveloped, unabscised post-anthesis flowers failed to set fruit. This type of apparent failure of fruit set commonly occurs among flowers which develop after considerable fruit set has already occurred on the clusters. They concluded that failure of unabscised flowers to set is due to an insufficient supply of nutritive materials and not to the lack of sufficient auxin for set since the auxin, parachlorophenoxyacetic acid (CPA), in combination with sucrose and ascorbic acid applied to those flowers resulted in an actual decrease in percentage set (33).

It was discovered that there is an inherent temperature sensitiv-

ity in the tomato ovary itself. Even in the presence of nutritive materials, excised flowers were shown to exhibit the same shape of temperature and sensitivity curves. Flowers on all media were treated with CPA in an attempt to force fruit set. It was found that the ability of flowers to set fruits on intact plants only within the temperature range of 10 to 30°C holds true for excised flowers as well. The addition of the two substances, sucrose and ascorbic acid, gave increased fruit set at every temperature tried and extended the temperature range over which fruit set could take place (33).

Growth of the ovary before anthesis is mostly by cell division, and after fertilization, growth is predominantly by cell enlargement (41). The stimulus which ensures the continuity of fruit enlargement through the anthesis period comes from the pollen (70). Associated with fruit set is a rapid surge of growth, beginning with the fertilized ovules. The origin of the stimulus is presumably from endogenous growth substances produced by the fertilized ovules (69). Pollen also inhibits the development of the abscission layer which would bring about flower drop in addition to stimulating the growth of the fruit itself (70). In a controlled pollination study, flowers not pollinated after emasculation always dropped off in a week or ten days from the time of emasculation (17).

Effect of Endogenous Auxin Levels. According to Johnson and Hall, under normal environmental conditions, pollination of tomato flowers occurs before the critical stage of auxin content is reached and the development of the ovary then restores the auxin level of the fruit which prevents the formation of the abscission layer. They hypothe-

sized that under high temperature and high light intensity, the critical stage effecting lowered auxin content and increased ethylene production is reached earlier and prior to the restoration of auxin attending pollination (26). The criteria employed by Leopold and Scott for determining when set had occurred was observing for loss of grooves between carpels 7 days after treating with auxin to induce fruit development; an ovary typically has such grooves, whereas, a set fruit loses the grooves at once (33).

Luckwill used the stimulation of tomato ovary growth as a bioassay for auxin extracted from apple seed endosperm by applying the substance to unpollinated tomato ovaries and measuring the enlargement 6 days after treatment. By comparing the growth of the ovaries to that from known doses of 2-naphthoxyacetic acid (2-NOA), the hormone content of the seed can be calculated in terms of 2-NOA. The substance tested is known to be an auxin since it is also active in the avena curvature test (36).

Gustafson proposed the hypothesis that the reason some fruits develop without seeds is that they have a high auxin content in the ovaries at the time of blossoming and that this is high enough to set off the growth processes with the result that the ovary commences to grow even though there has been no fertilization. Six cultivars of orange (Citrus sinensis), two seeded and four seedless, were used to compare auxin content of ovaries from buds. The seeded varieties contained less auxin as measured in indole acetic acid equivalents by the Avena coleoptile curvature test. Seeded lemon (Citrus limonia) also contained less auxin than seedless of the same species (18).

Crane proposed that the developing seeds with their attendant high levels of hormones act as mobilization centers of nutrients required for their growth and that of the surrounding fruit tissues (11).

Carbohydrate Changes. If pollination is prevented, no significant change in starch and reducing sugar content occurs during a period of two to three days after anthesis. As early as 48 hours after pollination, there was a marked increase in starch content of the ovaries, a slight increase in reducing sugars and a noticeable decrease in sucrose (37).

Parthenocarp

Some tomato cultivars will bear parthenocarpic fruit. For the particular variety studied by Osborne and Went, 'Essex Wonder', only low temperature combined with high light intensity and long photoperiod resulted in the formation of naturally parthenocarpic fruit (43). Young reported that usually most tomato fruits are seedless when set near 32.2°C (73). During late July, August, and September when the temperature was averaging over 29.4° (with the maximum often over 37.8°) and with the average relative humidity around 60%, it was observed that fruits of all selections that were still producing had very few or no seeds, while fruits of both 'Red Cherry' and 'Large Cherry' contained the usual numbers of seeds. Later, after cooler weather set in, fruits from these plants again had seeds (71).

Johnson and Hall grew 'Marglobe' along with several summer-

setting genotypes as a summer crop, spraying parachlorophenoxyacetic acid (4-PCA) to try to induce set. Although the summer-setting selections set throughout the high temperature period while 'Marglobe' did not respond to 4-CPA, the first seeded fruit in the summer-setting genotypes resulted from clusters tagged between Sept. 19 and Sept. 21 (6 days after the onset of cooler temperature), but 'Marglobe' did not produce seeded fruit until early October (3 weeks after the onset of cool temperature) (27).

Seed Development

Kretchman observed that fruit weight was closely associated with seed number (29). Tomatoes produced from large amounts of pollen were large and regular, produced a large number of seeds and did not fail to come to maturity in a single instance; while those from small amounts were smaller in size, had fewer seeds, were not so regular in shape and several stopped growing about the size of a pea. One-sided fruit developed from pollinating on only one side of the stigma (17). Also, Dempsey and Boynton reported a strong correlation between number of seeds per fruit and size of fruit (13). Heritability for seed set was low at high temperature (15).

The seed is embedded in a homogenous mass of thin-walled, loose parenchyma-like cells, which fills the locular cavity when the fruit is mature. This tissue appears very early in the development of the fruit, being first noticed as a small mound of primordial cells 60 hours after pollination. It is formed by an outward growth from the placenta, and gradually grows up around the seed on all sides,

finally wholly engulfing the seed. It presses against but does not unite with the outer and radial carpel walls (57). Natural parthenocarpic fruits showed no development of internal gelatinous tissue and were wholly parenchymatous (43).

Use of Growth Regulators

A number of auxins and several gibberellins have been found to induce development of seedless tomatoes of various quality compared to normally fertilized fruit (63). Only under conditions in which the plant is physiologically able to bear fruit, though temporarily infertile may a growth substance stimulate ovary development (43). At higher than optimum day and night temperatures, however, growth regulators fail to induce set (43).

Auxins have long been known to play an active role in fruit growth since the chief centers of auxin production in fruits are the seeds (63). Also, auxins (41) and gibberellins (63) have been reported to stimulate growth of the pollen tube. Since the 1940's, β -naphthoxyacetic acid (NOA) and parachlorophenoxyacetic acid (CPA) have been successfully used on a commercial scale in some areas to set fruit on plants grown at lower than optimum temperatures for set. P-chlorophenoxyacetic acid is used at a concentration of 50 ppm (69). In tomatoes, gibberellins stimulate growth, flowering, and fruit set. Setting of normal and of parthenocarpic fruits was increased by repeated floral sprays at concentrations ranging between 1 and 500 ppm (63).

Hollow fruits frequently developed as a result of NOA spray

treatment (43). The active synthetic growth regulating substance gave some development of gelatinous tissue in parthenocarpic set (43). Janes (25) compared the chemical differences between parthenocarpic fruits (set with indole acetic acid or indole butyric acid) and fruits set with pollen. He found that the pH of the juice from ripe seeded fruit was slightly lower than that from ripe parthenocarpic fruit while the locules of red ripe parthenocarpic fruits contained 1.5% more sugar than the locules of similar seeded fruit. Also, all other regions of the red ripe parthenocarpic and seeded fruits are mostly located in the locules suggests that the developing seeds exert a profound influence upon the chemical composition of the fruit, but this was found not to be the case (26).

Environmental Effects on Pollination, Fertilization, and Fruit Set

Humidity may be an important factor since Cooper discovered large stomata sparsely scattered over the style (8). Scott and George reported seed production was maximal when flowers at anthesis were pollinated during cloudy weather with relative humidity about 70% and temperature around 24°C (54). Kretchman earlier reported the optimum relative humidity for pollination and fertilization and subsequent fruit development is about 70% (29). In a study of longevity of stored pollen of the cultivar 'San Marzano', McGuire found that pollen collected during a period of hot, dry winds showed short longevity when used in pollinations compared to pollen collected under more favorable conditions. He stated that humidity seems at least as important as temperature in the preservation of tomato pollen, and the results show the most effective storage conditions being low temperature (0°C) and low

humidity (provided by storing in a capsule vial containing CaCl_2) (39).

Moore and Thomas transplanted 'Stokesdale' tomato plants to the field and compared plant growth and yield of those grown in full sun to shaded plants receiving 1/2 available light or 1/4 available light. The fact that reducing the light intensity had little effect on the air temperature under the shaded plots yet great effect on increasing fruit set and early yield, indicates that high temperature alone was not the only factor associated with the poor fruit set on the first two clusters. The results strongly suggest that the combined effect of high light intensity and high temperature, or solar radiation, are associated with poor fruit set. During first and second cluster bloom, air temperature averaged well above 32.2°C maximum and 21.1° minimum. The plants in either of the reduced light intensity plots had a greater leaf area than the plants in full sun. The plants under medium light intensity were taller and more stocky than those under high light intensity at the time the second clusters were in bloom. Plants that received medium shade gave higher yields over both low and high light plants from first and second cluster flowers for both parachlorophenoxyacetic acid (CPA) sprayed and unsprayed treatments (40).

Growth of the indeterminate types ('Marglobe' and S-1119N, a summer-setting selection) under high temperatures was extremely slow compared with their later growth at lower temperatures. Mature leaves and growing-point regions of all types, whether sprayed with parachlorophenoxyacetic acid (CPA) or unsprayed, were twisted and distorted and exhibited symptoms like those of typical 2,4-D damage.

'Marglobe' plants in the unshaded section of the greenhouse failed to set fruit even with CPA sprays, while the plants in the shaded portion set fruit with CPA sprays even though the temperature (generally in excess of 43.3°C) was essentially the same in both cases. This suggests that high light intensity is more critical (perhaps by inactivation of auxin) than high temperature, provided that auxin is supplied (26). Temperatures of $30\text{--}35^{\circ}\text{C}$ during only 4-6 hours per day on most days may not prevent setting of a fair crop of fruit in cloudy weather (72).

'Marglobe' plants transplanted in April and set out in full sun showed a severe check in growth by June 1, 1952. The effect of summer-induced dormancy upon growth rate was apparent once growth had been subsequently induced by either shading or leaf removal. High light intensity affects both growth and fruiting in the tomato by limiting stem elongation and by inducing a type of dormancy in fertilized or non-fertilized young fruits. Both effects could be partially reversed by either shading, defoliation, or CPA applications and hence appear to be related phenomena. The fact that shading or defoliation of tomato plants exposed to natural conditions of high light intensity alleviated the growth and fruiting inhibition suggests that the leaves are implicated, possibly as the primary photoreceptor (27).

The continued accumulation of leaf carbohydrates under summer conditions conducive for high respiration suggested that the curtailment of growth and fruiting involved an auxin-light reaction largely independent of photosynthesis. It was found that some of the respon-

ses of the 'Marglobe' tomato to natural summer conditions in Texas can be duplicated by far-red irradiation of plants grown in the greenhouse at normal temperatures during the winter months. By removing the blue cellophane from lamps producing the far-red treatment and shifting the radiation predominantly into the red (5800-7000 Å) the far-red inhibition was reversed, and subsequently formed tissues were normal. Far-red radiation inhibited cell elongation of the main stem resulting in shortened internodes. Microscopic examination of pollen from far-red irradiated plants indicated a high degree of non-viable grains. Far-red also appears to retard the abscission of unfertilized flowers. The effect of far-red upon pollen and flower abscission may be mediated through its effects upon the auxin-receptor complex. The effects of light on the oxidation of IAA and the interaction of red and infrared radiation, therefore, should be given considerable weight in evaluating the causes of summer-induced dormancy in tomatoes (28).

Environmental Effects on Style Elongation

Many researchers have studied the effects of style length on fruit set. In the tomato the stigma is enclosed within the united anther column in many varieties, and the introrse dehiscence of the anthers ensures self-pollination. Most tomato varieties developed in warm tropical or sub-tropical regions such as Peru or Mexico have a slightly exerted style so that cross-pollination by insect vectors occurs frequently and the amount of outcrossing between fully self-fertile lines may be as high as 26%. By contrast most of the adapted

varieties of temperate latitudes have an inserted style and the amount of outcrossing is very low (68).

Smith reported that under high temperature, styles elongated before flowers opened and anthers dehisced (56, 57). Burk reported that 'Bonny Best' failed to set fruit when pistils were exerted 1/16 to 3/16" longer than stamens although the pollen and pistils were found to be functional (6). Levy reported that no fruit set was ever observed when styles protruded more than 1 mm out of the antheridial cone and stated that there exists a strong relationship within each line between flower drop and style exertion: the longer the style, the higher percent flower drop under field conditions (35). Charles and Harris found the distance between the top of the antheridial cone and the stigmatic surface was greatest at low temperature and decreased with increasing temperature in all selections tested. They further concluded that at 26.7°C, the high level of the stigma in the antheridial cone was the main factor reducing fruit set (7).

In a study of mutants of 'San Marzano', a mutant line (ex. 47L2-191) was discovered that had greatly elongated styles and consequently exerted stigmas. The stigma of most of the flowers projects 1-5 mm beyond the end of the anther tube. Pollen was seen on the style and stigma of 2 of 21 mutant ex. flowers in the sample while 18 of the flowers had pollen on the style only (47). In the sample of 55 flowers of normal fruitful tomatoes examined under a dissecting microscope, pollen could be detected on styles of 52 and on stigmas of 49.

Rick and Dempsey made the correlation that the lower the stigma

level, the higher the fruit set (48). However, El Ahmadi eliminated style exertion as a barrier to pollination since one of his test genotypes, PI 262934, which exerts its stigma at high temperature gave the highest fruit set of all those tested (14). Scott and George reported that style insertion is detrimental to fruit set. Yield decreased with increasing stigma insertion in all field populations (53). However, they found that selfing of exerted flowers for seed production without emasculating is limited to less than 4% if the flowers were pollinated by hand at anthesis (54). Coyne reported that under soil moisture stress, two of five cultivars tested showed a significant increase in style length, and one of these two cultivars had styles extending beyond the anther cone. However, pollination of these elongated pistils must have occurred because good fruit set was observed (10). Johnson and Hall reported that their 'Marglobe' plants showed stilar exertion throughout the high temperature period, and normal styles were not observed until September 25, 12 days after the onset of cooler temperature (26).

Style elongation has been reported to result from factors other than high temperature. Howlett induced carbohydrate deficiencies in tomatoes and found that at high N/low C ration, styles elongated. He stated that short pistils were favored by high light intensity, long photoperiod, and moderate N which would induce a high C:N ratio (22). Burk had earlier discovered that photoperiod affects style length in greenhouse tomatoes. 'Bonny Best' and 'Princess of Wales' were grown in a greenhouse at 8 and 16 hours daylength. 'Princess of Wales' developed inserted styles and set fruit at both daylengths.

'Bonny Best' developed inserted styles and set fruit at 16 hours daylength but developed exerted styles (1/16 to 3/16" longer than the staminal tube) and failed to set fruit at 8 hours daylength (6).

Style length is dependent on the genotype and varies widely within a genotype (26). Howlett reported that within a variety, the relative length of the pistil and stamens was observed to vary from flower to flower within a single cluster, from cluster to cluster, and from plant to plant (22). Burk attempted to prove transgressive inheritance of short pistils (6). Scott and George concluded that stigma exertion was incompletely dominant to insertion, and in all crosses the resulting hybrid stigma positions were skewed toward the exerted parent (53). Levy reported the heritability ($H=43\%$) of style exertion in the cultivars 'Hotset' and 'Gamad' and in the F_1 and F_2 generations of the crosses between them (35). Rick and Dempsey reported that stigma length is determined by quantitative inheritance by relatively few genes (48). Ruttencutter and George found nine loci controlling insertion (51). Stigma exertion at high temperature is controlled by partially dominant genes with a high diallel additive component and heritability (15).

High Temperature Effects on Plant Cells

Many micrometeorology experiments have shown that in the field, the plant is rarely at air temperature. The plants are often warmer than the air during the day and cooler at night. If the transpiration of plants decreases and if the radiation balance and wind structure maintain the same, the decrease in latent heat exchange will result

in an increase in plant temperatures. Alfalfa temperatures $5-10^{\circ}\text{C}$ below air temperature at night and $5-10^{\circ}\text{C}$ above air temperature during parts of the day have been frequently observed (60).

Changes of metabolism that cause injuries or even death of a plant occur under the influence of high temperature (16). Thermostability of plant cells is due to the resistance of their proteins to denaturation, resistance to injurious metabolic changes, respiratory capacity, and capacity to harden. The thermostability of the proteins is constant in higher plants. Secondary denaturation occurs when the agent causes metabolic changes and these changes in turn lead to denaturation of cell proteins (2). Changes of metabolism in particular are expressed in decomposition of crucial bipolymers (nucleic acids, proteins) with synthesis of toxic ammonia. The heat resistance of plants increases after reactivation of protein synthesis, during increase of organic acids and bound water in the cells, and during increase of protoplasmic viscosity. A number of chemical substances are now known to increase the resistance of plants to high temperatures. Of physiologically active substances, adenine exerts such an effect (16).

Criteria for the determination of life in plant tissue at a cellular level as this is affected by heat damage or high-temperature tolerance are of several sorts: plasmolysis, cell necrosis, and protoplasmic streaming. Visual detection of cell necrosis reveals gross modifications in cytoplasmic structure, including the development of Brownian movement of particles, the precipitation of cellular inclusions, and the appearance of cellular degradation products such

as tannin bodies. These observations are considered to indicate irreversible changes in cellular organization that imply a state of nonfunction or death in the cell (52).

A number of crop species were tested for heat tolerance by electrolyte leakage from leaf discs bathed in deionized water and measuring electrical conductivity. The temperature range of 44.2-48.4°C was found to cause 50% injury after 1 hour exposure using full grown plants of tomato (59).

High Temperature-Setting Varieties

Less than 1% of the world collection of the garden tomato (Lycopersicon esculentum Mill.) and related Lycopersicon species displayed a high level of heat tolerance based on fruit setting ability at high temperature. About 80% of tomato accessions tested set almost no fruit during the warm months (64). The Asian Vegetable Research and Development Center (AVRDC) has grown and screened 4616 tomato accessions in the field for heat tolerance. Thirty-nine of them have been found to be heavy fruit setters at high temperature, and these cultivars which originated from 15 countries can be used for developing heat-tolerant varieties. TAMU-Chico III ranks 7th among these genotypes with a rating of 4.2 on a 1-5 scale for fruit-setting (65).

Experiment findings suggest that the heat-tolerant genes are easily influenced by environment and may involve shade tolerance, pollen heat-tolerance, stylar exertion, and parthenocarpy. Field experiments were conducted at AVRDC to determine the inheritance of

heat-tolerance. Results suggest a fairly complex inheritance of heat-tolerance. Heritability values were generally low, ranging from 5-19%, which indicates that the greater proportion of variability observed was due to environmental causes (65). Diallel test results showed that heat tolerance is under heritable mechanism, conditioned by an additive gene system with some dominance (19).

TAMU Chico III

The TAMU Chico III tomato is a pear-shaped, processing-type tomato adapted to machine harvest. TAMU Chico III was developed at the Texas A&M Agricultural Research and Extension Center at Weslaco by Paul W. Leeper. The variety will set fruit at high temperatures: 24.4-25°C night and 35.6-36.1°C day (31).

TAMU Saladette

TAMU Saladette was developed at the Texas A&M University Agricultural Research and Extension Center, Weslaco, Texas by Paul W. Leeper. Small determinate vines, concentrated fruit set, concentrated maturity and fruit toughness enables TAMU Saladette to be machine harvested as either a fresh market or a processing variety. Fruit of TAMU Saladette are small averaging about 2 ounces in weight.

TAMU Saladette sets fruit over a very wide range of temperature and humidity conditions. During testing TAMU Saladette set commercial acceptable crops of fruit when daily maximum temperatures were in the range of 35° to 37.8°C and night temperatures never lower than 25.6° to 26.7°C. Fruit set has been good even when

high relative humidity and high temperature conditions prevailed together. The high temperature setting ability of TAMU Saladette has enabled the production of tomatoes from 4 to 6 weeks later into the summer than is possible with any other fresh market variety (32).

Freshmarket 9

Freshmarket 9 was developed at the Texas A&M University Agricultural Research and Extension Center at Weslaco by Paul W. Leeper. The most outstanding characteristic of Freshmarket 9 tomato is its ability to set fruit over a wide range of temperature and humidity. This characteristic results in extended production periods in both spring and fall grown crops as well as larger yields.

In yield test, Freshmarket 9 was found to be more productive than either of the commercial varieties, MH 1 and Flora-Dade, and fruit size was larger. Freshmarket 9 also has an earliness advantage over the checks; a full month earlier than either in fall and one week earlier than MH 1 and two weeks earlier than Flora-Dade in spring.

Freshmarket 9 displayed the largest advantages over the commercial checks in the summer trials where high temperatures were experienced. High yields resulted when fruit was set while maximum and minimum temperatures exceeded 35° and 23.9°C , respectively and relative humidity was high (32).

MATERIALS AND METHODS

Selection of Genotypes

Fifteen genotypes were selected from crosses of Mr. Paul Leeper's tomato breeding program at the Texas Agricultural Research and Extension Center, Weslaco. Genotype selection for study was based on varying ability to set fruit at high temperature. Plants were screened at Weslaco on July 15-17, 1980 following daily maximum temperatures greater than 33°C for the preceeding 6 weeks while daily minimum temperatures during the same period exceeded 22°C. Forty-four genotypes were clasified according to fruit and flower number on the lower, middle, and upper part of the plant. From the 44 genotypes screened, 15 were further evaluated for pollen dehiscence, and in vitro pollen germination percentage and style length relative to the antheridial cone was measured.

On August 8, 1980, seeds of the 15 genotypes were sown in vermiculite in a greenhouse in College Station and transplanted to the field on September 13 in a completely randomized block design with 3 replicates. Of the 15 genotypes screened from the initial study, 6 genotypes ['9', '98', '106', '110', '200', and 'Flora-Dade (FD)'] were selected for measurements of in vitro pollen germination and style length.

On December 3-4, 1980, measurements of in vitro pollen germination percentage and style length were made for 6 genotypes ('9', '98', '106', '200', 'FD', and 'Chico III') growing at Weslaco.

On February 13, 1981, seeds of 9 tomato genotypes ('9', '98', '106', '110', '200', '229', 'FD', 'MH 1', and 'Chico III') were sown in the greenhouse in College Station with the exception of '9' and

'MH 1' which were sown February 26. Seeds were sown in a peat-lite medium in individual cells of plastic flats. Seedlings were thinned to 3 seedlings per cell. Seedlings were hardened off for 2 weeks outdoors between greenhouses until after the danger of frost had passed. On April 2, 1981, plants were transplanted to the horticulture farm field. A total of 9 genotypes were planted 3 seedlings per hill in 3 replicated completely randomized blocks. Spacing distance was 0.46 M between plants within blocks, each of 3 rows having 9 blocks. Plants were grown 3 seedlings per hill at 0.46 M spacing to simulate density of commercial direct-seeded tomatoes in the Lower Rio Grande Valley.

It was decided to include '229', one of the original fifteen genotypes although similar to '200' because, under high temperature conditions of 1980 at Weslaco, it exhibited the highest percentage of exerted styles (90%) of all genotypes, and all of its fruit was parthenocarpic.

Of the 9 genotypes grown in College Station in the spring of 1981, which also includes the 5 used in embryological and pollen germination studies, 2 are commercial check varieties: 'MH 1' and 'Flora-Dade'. 'Chico III' is a TAES release and is now one of the most widely grown processing tomatoes in the world. 'Freshmarket 9' ('9') is a 1981 TAES release. Genotypes '98', '106', '110', '200', and '229' are breeding selections of Mr. Paul Leeper at the Texas Agricultural Research and Extension Center at Weslaco. Freshmarket varieties are 'Freshmarket 9', 'Flora-Dade', and '110'. The others are processing types: '98' and '106' fruits are rounded; '200', '229', and 'Chico III' fruits are pear shaped. All are determinate in growth (Appendix Table 1).

For the spring 1981 crop grown in College Station, seeds were sown

in the greenhouse and transplanted to the field, taking about 120 days from seed to mature fruit. The 1980 crop at Weslaco was direct-seeded on April 16, and mature fruit was observed on July 15, 61 days after seeding. The 1981 Weslaco crop was direct-seeded on March 6 and mature fruit was observed on July 2, 68 days after seeding.

Techniques

(1) In Vitro Pollen Germination

Anthesis flowers having yellow reflexed petals were collected. Pollen of 5 flowers per genotype was cultured on slides containing Brewbaker and Kwack medium. Each slide was then covered in a petri dish containing moist filter paper to keep from drying out. Four hours after plating, 1000 pollen grains were observed for germination under a light microscope at 400x. Percent pollen germination was recorded.

(2) Style Length Measurements

To measure stylar insertion/exsertion, the distance from the stigmatic surface to the top of the antheridial cone was recorded in mm using a dissecting microscope and a 1 cm ocular micrometer having a scale of 100 increments. A positive value was given if the stigma protruded beyond the anther cone, and a negative value was given if the stigma was below the anther cone. A sample size of 30 flowers was taken for each genotype.

(3) Fruits Observed

For each of the field plantings studied, after the first set fruit had ripened, samples of fruit of all sizes, from lower clusters to young fruit at the top of the plant, were collected, cut in half, and

observed for seed and gel development.

(4) Histological Studies of Embryo Sacs and Pollen

Anthesis stage flowers of the genotypes '9', '110', '200', '229', and 'FD' were collected at temperatures favorable for fruit set before the temperature exceeded 31.7°C (Spring 1981) during flower development and compared with flowers from plants grown at temperatures reaching and exceeding 37.8°C (Summer 1980).

Flowers were fixed in formalin-acetic-alcohol (FAA), dehydrated, mounted in Paraplast Plus^R blocks and sectioned with a microtome knife at 12 µm in thickness. Before dehydrating, calices and corollas were removed with forceps, leaving only the pedicel and reproductive organs. Transverse and longitudinal sections of flowers were used to examine pollen dehiscence from locules and embryo sac development. Sections were mounted serially on slides and stained with safranin-fast green and observed under a light microscope.

(5) Relation of Flower Bud Length and Meiosis to Days to Anthesis

Plants for the study were grown in field plots in College Station in the spring of 1981. All flower buds of five inflorescences of each of the 9 genotypes ('9', '98', '106', '110', '200', '229', 'FD', 'MH 1', and 'Chico III') were measured to the nearest 0.1 mm using a caliper and tagged on May 27. Each day thereafter until all flowers had opened (June 6) inflorescences were observed and the date was recorded when each flower bud reached anthesis as determined by yellow reflexed petals. A linear regression equation was derived to correlate bud size with number of days to anthesis.

Microsporogenesis stages were determined for different pre-recorded flower bud sizes by excising immature anthers from flower buds collected in 3 absolute ethanol:1 glacial acetic acid. Anthers were squashed on a slide in a drop of aceto-carmin stain and observed at 400x under a light microscope.

RESULTS

In Vitro Pollen Germination

Percent in vitro pollen germination at progressively higher temperatures were recorded over a 14 day period preceeding testing (Table 1). The early season tests (May 10, 1981) showed the highest percent germinability for all genotypes. Morphologically normal pollen appeared round and had 3 nipples, and sterile pollen appeared football-shaped (Fig. 1). Genotype '110' had the most constant pollen viability: high-temperature-(July 16, 1980)-pollen was not significantly different in percent germination from pollen developed under favorable temperature (May 10, 1981).

On July 16, 1980, A.M. and P.M. pollen counts were made (Table 1). Genotype '110' had a significantly higher germination percentage at P.M. while genotypes '200' and '106' only germinated during A.M. Pollen counts for genotype '229' were very low at both times. For the other genotypes ('9', 'FD', and '98'), no germination occurred at the P.M. count.

Style Elongation

Style lengths of flowers from several genotypes from 3 different crops are shown in Table 2. There was a general increase in style length (less negative value in style length relative to the antheridial cone) with increasing temperature prior to anthesis, with the exception of genotypes '98' and '106', between December 3, 1980 and May 10, 1981.

With increasing temperature, the percentage of flowers having exerted styles increased, and all genotypes except '110' had some exerted styles at the July 17, 1980 measurement. Genotype '229' had

Table 1. "In vitro" germination percent of pollen developed at various temperatures as determined by observing tube growth of pollen 4 hours after plating on Brew-baker and Kwack media at room temperature.^z

Date	Temp. ^y	9	110	200	229	FD	98	106	Chico III
May 10, 1981	31.7 ^o	42.6 ^a	56.3 ^a	18.0 ^{ab}	29.2 ^a	37.6 ^a	39.0 ^a	43.4 ^a	51.8 ^a
May 18, 1981	30.6 ^o	28.8 ^b	38.9 ^b	15.7 ^b	25.0 ^a	27.9 ^b	34.0 ^a	30.1 ^b	30.0 ^b
June 6, 1981	32.8 ^o	16.7 ^c	46.4 ^{ab}	6.8 ^{bc}	<1% ^b	0.0 ^c	0.0 ^b	11.8 ^{cd}	<1% ^c
July 16, 1980 (A.M.)	37.8 ^o	----	42.8 ^b	26.7 ^a	2.0 ^b	----	----	21.3 ^{bc}	----
July 16, 1980 (P.M.)	37.8 ^o	0.0 ^d	56.6 ^a	0.0 ^c	0.5 ^b	0.0 ^c	0.0 ^b	0.0 ^d	----

^zMean separation within columns by Duncan's multiple range test, 5% level.

^yHigh temperature over 14 days preceeding germination test date.

Fig. 1. In vitro pollen germination after 4 hrs. on Brewbaker and Kwack media. A. germinated pollen grain with tube. B. morphologically normal and sterile pollen grains.

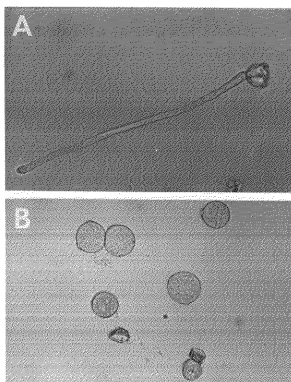


Table 2. Style length measurements made on flowers that developed over different temperatures.

Date & temp. ^z	Genotype															
	9		110		200		229		FD		98		106		Chico III	
	mean	% ex ^w	mean	% ex	mean	% ex	mean	% ex	mean	% ex	mean	% ex	mean	% ex	mean	% ex
Weslaco Dec. 3, 1980 26.7 ^o C	-1.52 ^{byx}	0	----	--	-1.46 ^b	0	----	--	-2.25 ^c	0	-2.25 ^c	0	-1.69 ^c	0	-3.05 ^c	0
C.S. May 10, 1981 31.7 ^o C	-0.75 ^b	0	-3.41 ^c	0	-1.43 ^b	0	-0.32 ^b	20.0	-1.47 ^b	0	-2.51 ^c	0	-2.22 ^d	0	-2.00 ^b	0
C.S. June 7, 1981 32.8 ^o C	-0.25 ^b	20.0	-1.83 ^a	0	-1.03 ^b	0	+0.15 ^b	50.0	-1.19 ^b	0	-0.82 ^b	0	-0.78 ^b	0	-0.98 ^a	0
Weslaco July 17, 1980 38.3 ^o C	+4.51 ^a	66.7	-2.18 ^b	0	-0.13 ^a	46.7	+1.70 ^a	90.0	+2.19 ^a	68.0	-0.11 ^a	25.9	-0.17 ^a	26.7	----	--

^zHigh temperature over 14 days preceeding measurements.

^yDistance from stigma to top of antheridial cone (- denotes inserted; +, exerted).

^xMean separation within columns by Duncan's multiple range test, 5% level.

^wPercent of flowers sampled having exerted stigmas given for each genotype sampled.

the highest percentage of exerted flowers (90%) at the highest temperature (Table 2, Fig. 2E). Genotype '110' had inserted styles at all temperatures (Table 2, Fig. 2C). Genotype 'FD' is shown having a slightly inserted style (Fig. 2F) and with an exerted style and a split anther tube (Fig. 2G) as was common at high temperature.

Fruit Set and Parthenocarpy

The average maximum temperature over 7 weeks prior to collecting fruit in the summer of 1981 was 33.1°C while the lowest maximum temperature over the same period was 28.3°C (Fig. 3(A)-7(A) & Fig. 8). Corresponding temperature data from the summer of 1980 shows an average maximum of 37.1°C with the lowest maximum at 33.3°C (Fig. 3(B)-7(B) & Fig. 8).

Mature fruits of genotypes '9' and '110' on July 17, 1980 [Fig. 3(B) & 4(B)] appeared normal, containing locules filled with seeds and gel while progressively smaller fruits in the same photos showed some empty locules containing few or no seeds and lacking gel. On July 17, 1980, fruits of genotypes '200' and '229' at all stages from red ripe to small green were all entirely devoid of seeds and gel and as a result were much more lobed than rounded [Fig. 5(B) & 6(B)]. Plants of genotype 'FD' did not contain any fruit at that time of collection.

Over the 50 day period before collecting fruits on July 2, 1981, the maximum daily temperature, reached on 3 consecutive days, was 35.6°C (Fig. 8). Yet, fruits of all 5 genotypes, from recently set to mature ripe, contained seeds and gel [Fig. 3(A)-7(A)]. Genotype 'FD' produced fruits over this temperature range but did not the previous season (July, 1980).

Fig. 2. Inserted/exserted flowers. A. '9' slightly exserted. B. '9' very exserted. C. '110' inserted. D. '200' inserted. E. '229' exserted. F. 'FD' slightly inserted. G. 'FD' exserted with split anther tube.

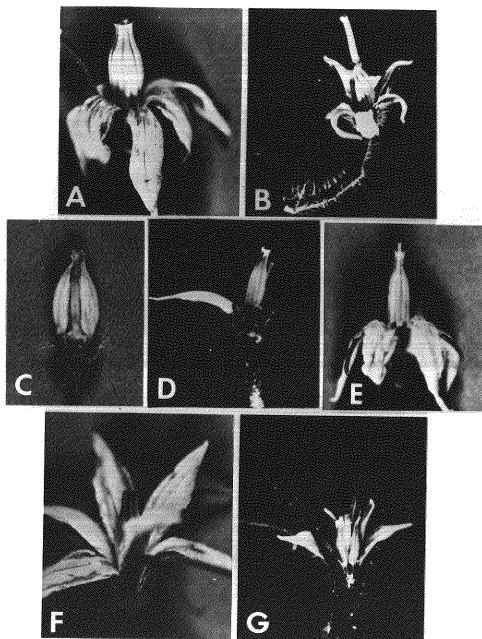


Fig. 3. '9'. Fruits collected at different temperatures. A. July 2, 1981. B. July 17, 1980.

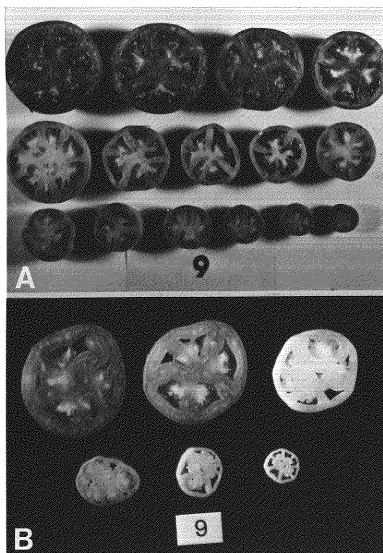


Fig. 4. '110'. Fruits collected at different temperatures. A. July 2, 1981. B. July 17, 1980.

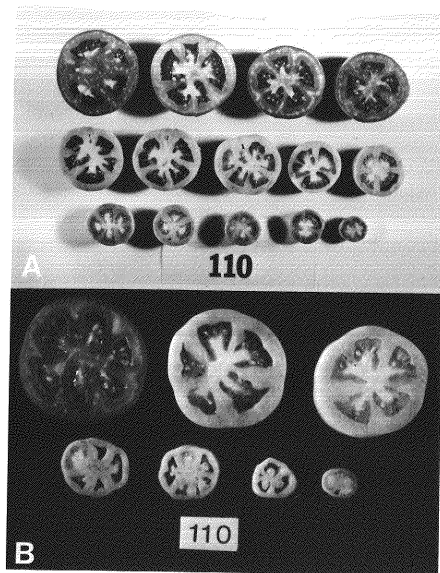


Fig. 5. '200'. Fruits collected at different temperatures. A. July 2, 1981. B. July 17, 1980.

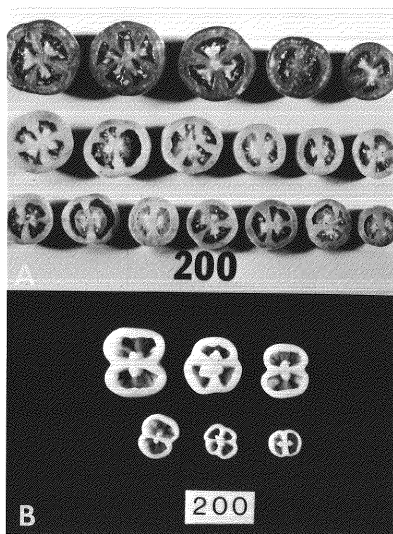


Fig. 6. '229'. Fruits collected at different temperatures. A. July 2, 1981. B. July 17, 1980.

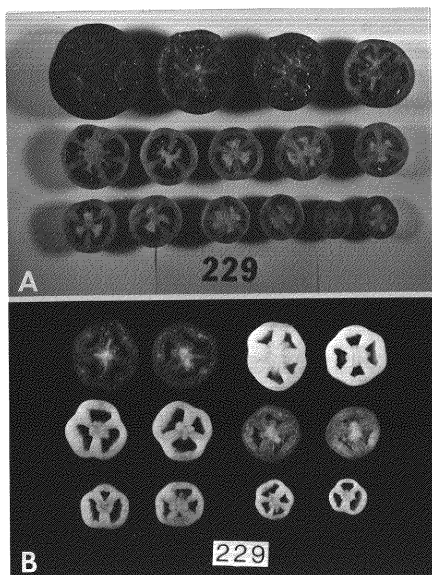
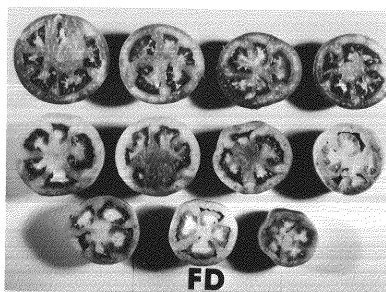


Fig. 7. 'FD'. Fruits collected at different temperatures. A. July 2, 1981. B. July 17, 1980.



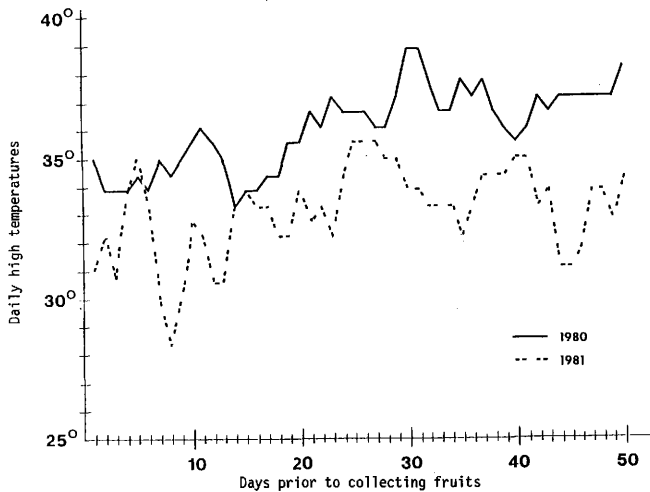


Fig. 8. Temperatures during fruit set for two summers at Weslaco, Texas.

Embryo Sac Viability

Anthesis stage flowers were collected on May 1 and May 20, 1981 in College Station and July 16, 1980 at Weslaco. Ovary sections from these flowers were observed to determine if embryo sacs were viable or degenerated (Fig. 9). In all 5 genotypes, both viable and degenerated-like embryo sacs were found in the May 1981 flowers. Ovary locules of 'FD' July 1980 flowers were malformed, appearing as cabbage-like leaves.

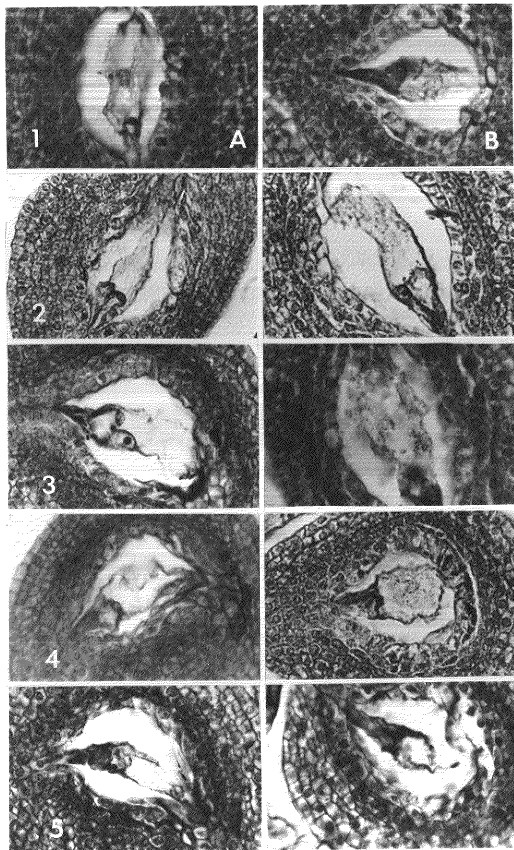
High temperature during development of May 1 and May 20, 1981 flowers did not exceed 32.2°C while the average maximum temperature over the 14 days prior to collecting the flowers was 27.2°C . High temperature during development of July 1980 flowers was 37.8°C while the average maximum temperature over the 14 days prior to collecting was 36.9°C (Fig. 10).

Pollen Dehiscence

Anthers from flowers of genotypes '9', '200', '229', and 'FD' collected on July 16, 1980 were sectioned in transverse plane to determine if anther lobes were dehiscing pollen at high temperature. Previous investigators reported that fewer pollen grains are produced and released at high temperature (1, 14, 35), and that the dehiscence split in the anther wall may not occur (14, 50).

From observations of genotype 'FD' anthers from May 1981 and July 1980 (Appendix Table 2), it was concluded that the anther thecae of high temperature flowers does not break down to the degree that it does in flowers grown at favorable temperature so that passage of pollen from the microsporangial cavities is impeded as is its release from

Fig. 9. Longitudinal sections of tomato embryo sacs. Genotypes: (1) '9', (2) '110', (3) '200', (4) '229', (5) 'FD'. A. Viable embryo sacs of flowers collected May 1 or 20, 1981 in College Station. B. Degenerated embryo sacs from flowers collected July 16, 1980.



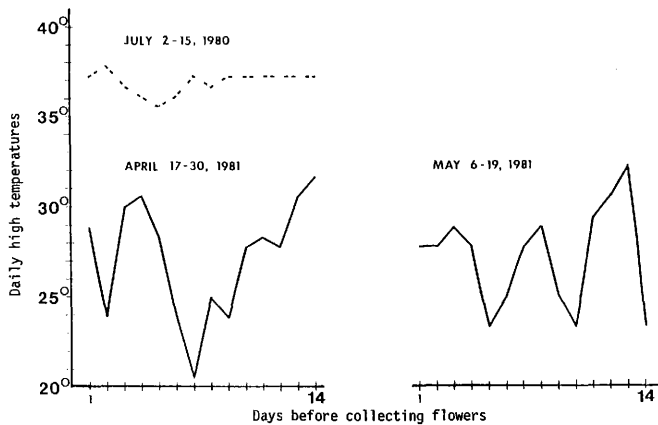


Fig. 10. Temperatures encountered by flower buds used in the study of embryo sac viability.

the anther lobe. In genotype 'FD', it appeared that much more pollen was contained in the anthers of favorable temperature (May 1981) flowers, and all of the grains appeared morphologically normal in sectioned material as compared to few pollen grains, many of which were sterile in high temperature flowers (July 1980). ,

For genotypes '9', '200', and '229', only July 16, 1980 anthers were observed so they cannot be compared to favorable temperature flowers during 1981. However, in most of these anthers, the connective tissue in at least one anther of each flower was broken down and appeared capable of releasing pollen although some flowers contained only sterile pollen (Appendix Table 2). Failure of endothecium thickening (50) did not appear in any of these genotypes examined.

Inflorescence Type

Five inflorescences of each genotype were examined to determine the type of inflorescence and the opening sequence of the flowers born on such. It was found that 2 basic types of inflorescences were represented: scorpioid cyme and racemose cyme (Appendix Table 3). However, in both types of inflorescence, most flowers contained an ovary which either enlarged or else remained in a static condition while few abscised. The raceme type inflorescence bore more flowers per inflorescence than did the cyme type, while in both types, every flower did not result in a fruit, but only the first few flowers to reach anthesis developed into mature fruit (Appendix Fig. 1).

DISCUSSION AND CONCLUSIONS

Pollen Germination

Pollen viability in Table 1 was determined by tube growth rather than morphologically since Howlett (21) reported observing morphologically perfect pollen grains which stained but failed to germinate on the stigma or the agar media. Note that pollen germination results presented in Table 1 are for the pollen cultured in vitro at room temperature. However under high temperature field conditions, one could expect reduced germination percentages on the stigma and slower tube growth down the style (57).

Style Exertion

Style exertion may have contributed to lower percent fruit set (6, 7, 35, 48) in genotypes '9', '200', '229', and 'FD' at high temperature in July 1980 at Weslaco. However, the gametophytes also were nonfunctional at those temperatures. The genotypes that had the lowest pollen percent germination at high temperature also had the highest mean style length and percent exerted flowers (Tables 1 & 2).

Temperature Effects on Fruit Set

Early to Mid-Summer of 1980 at Weslaco

Mature fruits collected on July 17, 1980 were probably set before mid-June while the smaller fruits were probably set the latter part of June [Fig. 3(B)-7(B)]. Daily maximum temperatures were greater than 33°C over the entire 50 day period and exceeded 35°C everyday from 31 days before collecting fruit up to the date of collection while the maximum temperature over this 31 day period reached 38.9°C (Fig. 8). The 31 day period should have been sufficient time for an ovary to go

from anthesis to mature fruit during summer (32). However, since gametogenesis and style exertion precede anthesis (23, 24, 50, 56, 57), a longer time period was examined.

Assuming temperatures of $>33^{\circ}\text{C}$ but $<35^{\circ}\text{C}$ during development of flowers that produced mature fruits in Fig. 3(B)-7(B) while the smaller fruits probably developed from flower buds exposed to $>35^{\circ}\text{C}$ and considering the data in Table 2, one can extrapolate that at such temperatures, a high percentage of flowers of genotypes '9' and '229' and possibly some '200' would have had exerted styles, a potential barrier to self-pollination and fruit set or seed set and gel development.

High temperatures during flower development probably also decreased pollen viability if one can extrapolate from Table 1 the effect on pollen developed at $>33^{\circ}\text{C}$ for larger fruits and $>35^{\circ}\text{C}$ for smaller fruits [Fig. 3(B)-7(B)]. Probably, only genotype '110' would have had a large percent viable pollen while no viable pollen could be expected for '229' and 'FD'. Genotype '9' would probably have had a low percentage viable pollen judging from the 16.7% viability at 32.8°C and no viable pollen at 37.8°C . Genotype '200' may have had some viable pollen since 26.7% viability was recorded at 37.8°C .

Summer of 1981 at Weslaco

Considering the high temperatures (5 days at 35°C and 3 days at 35.6°C) over the period preceeding fruit collection on July 2, 1981 and trying to extrapolate percentages of flowers having exerted styles and the percent pollen viability for each genotype leads only to the same conclusions as made for July 17, 1980 fruit since high temperatures ($>35^{\circ}\text{C}$) were encountered during both seasons. Therefore, if style

elongation and pollen viability did affect seed and gel development, the critical temperature must be between 35.6°C and 39.9°C if it is just a one day high temperature effect (23, 24, 50) rather than a longer period of high temperature.

Flower Bud Development Stages

Previous researchers determined that 9-5 days before anthesis and 1-3 days after anthesis were the bud stages most susceptible to high temperature after finding that meiosis occurs in the microspore mother cell 9 days before anthesis and 8 days before anthesis in the megaspore mother cell (23, 24, 50). In this study, time of occurrence of meiosis in microspore mother cells was determined to be from 5.6-8.1 days, depending on the genotype (Table 3). Microsporogenesis precedes megasporogenesis (9, 23, 24, 34, 57) so that the functional megaspore and megagametophyte develop nearer anthesis.

Flower Collecting and Sectioning

Flowers from plants grown under 2 different temperature regimes were collected for sectioning. The high temperature over 14 days before flowers were collected at anthesis reached 37.8°C for the 1980 Weslaco crop and 32.2°C for 1981 College Station crop (Fig. 10). Temperatures over 14 days were used to include the entire development period of the flower since yellow, reflexed flowers were collected, and flowers remain at anthesis for several days after the 5.6-8.1 days from microsporogenesis to anthesis (shorter time from megasporogenesis to anthesis).

Flowers were sectioned in both longitudinal and transverse planes.

Table 3. Correlation between flower bud development and days to anthesis.

Genotype	Bud length (y) (mm)	Days from meiosis ^z to anthesis (x)	Linear regression equation
9	5.0 - 5.9	6.9 - 7.9	$y = -.8844x + 11.9624$
110	4.6 - 5.7	5.7 - 7.0	$y = -.8710x + 10.6644$
200	6.2 - 7.0	7.5 - 8.1	$y = -1.1771x + 15.7864$
229	5.8 - 7.0	6.9 - 8.0	$y = -1.0598x + 14.2961$
FD	8.8 - 12.0	5.6 - 7.6	$y = -1.5878x + 20.8780$
98	5.2 - 6.0	6.6 - 7.5	$y = -.9629x + 12.4019$
MH I	7.5 - 7.6	6.9 - 7.0	$y = -1.0639x + 14.9332$
106	5.3 - 6.0	6.6 - 7.6	$y = -.73746x + 10.8962$
Chico III	6.2 - 7.0	6.9 - 7.6	$y = -1.1168x + 14.7102$

^zMicrosporogenesis

Transverse sections of anthers were needed to examine pollen dehiscence from locules. However, the best embryo sac sections were revealed in longitudinal sections of ovaries although some good embryo sac sections occurred in transverse.

Embryo Sac Degeneration

The main criteria for determining embryo sac degeneration was cell necrosis, including the precipitation of cellular inclusions and the appearance of cellular degradation products (52). As in avocado (61), the tomato degeneration observed concerned mainly the egg apparatus and less frequently the polar nuclei.

Assuming injury to an embryo sac results from protein denaturation or metabolic changes induced by high temperature (2, 16), the capacity of some embryo sacs of genotypes '9' and '110' to remain stable while those of others degenerated may be due to differential concentrations of organic acids and bound water in the cells or differential protoplasmic viscosity (16, 33).

From the results presented herein, it was concluded that both the microgametophyte and megagametophyte were adversely affected by high temperature. There appears to be genotypic variability as to which gametophyte is most affected. Genotype '229' gave 26.7% pollen germination from flowers that developed during temperatures reaching 37.8°C while ovaries collected at the same time showed degeneration of all embryo sacs. Genotype '110' had consistently high germination percentages over the entire temperature range. Small fruits of genotype '110' lacked seeds and gel, indicating that its embryo sacs are suscep-

tible to high temperature injury.

High Temperature Exposure Period

Time of occurrence and duration of high temperature could affect on gametophyte and not the other. This could be explained by the fact that microsporogenesis precedes megasporogenesis and that the meiotic stage (23, 24, 50) and pollen tube growth and fertilization stages (1, 23, 24, 55, 57) are most susceptible to high temperature. If the high temperature occurs only one day during microsporogenesis, the megaspores may develop normally. Conversely, if the high temperature occurs during megasporogenesis, the microspores may not be affected.

Typically, an inflorescence bears flower buds in different stages of development (8), and a plant will bear many inflorescences over a growing season. Thus, it would require high temperature over many consecutive days to incapacitate both male and female gametophytes, i.e. failure to set fruit or production of only parthenocarpic fruit (this was seen in genotypes '200', '229', and 'FD' in the summer of 1980 at Weslaco).

Environmental Effects

In this study, plants were grown under natural field conditions. It is not known what the effect of shading, defoliation or exogenous auxin spray (26, 27, 40) would have had on plant growth and fruit set of the 1980 Weslaco crop. According to Johnson and Hall (26, 27), a spray application of an auxin (CPA) could reverse the light inhibition, so it is possible that these genotypes ('9', '110', '200', and '229') are higher in natural endogenous auxin content than other varieties

as indicated by the ability to set parthenocarpic fruit (18) and that photo-oxidation of auxin is not occurring in these genotypes as it did in the test variety of Johnson and Hall.

Conclusion--Temperature Range

Data obtained in these experiments seems to indicate a sharp decrease in pollen viability from flowers developed above temperatures of 30.6°C with the exception of genotypes '110' and '200'. Style exertion appeared at temperatures above 32°C (Table 2) while few degenerated embryo sacs occurred in flowers that developed at 32.2°C. Fruit and seed set were excellent for all genotypes over an average maximum temperature of 33.1°C. At an average maximum of 37.1°C, no fruits developed on plants of genotype 'FD', while only parthenocarpic fruits were formed on plants of '200' and '229' and few partially seeded fruits were observed in '110' and '9'. Therefore, the upper range for these genotypes to set seeded fruit appears to be between 33.1°C and 37.1°C (Appendix Table 4).

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Appendix Table 1. Characteristics observed in the initial genotype selection on July 15, 1980 at Weslaco.

Genotype	Use	Fruiting Habit (relative no. and position)	Flower no.
9	fresh-market	few all along stem	low
110	"	medium no. all along stem	medium
200	processing	very few; only on lower 1/3	very high
229	processing	medium no. all along stem	high
FD	fresh-market	no fruit	very low

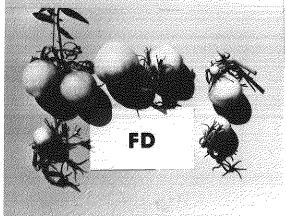
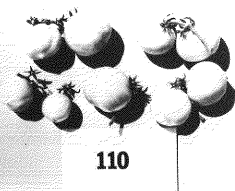
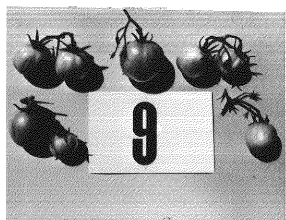
Appendix Table 2. Anthers observed in transverse sections.

Genotype	Flower no.	Connective tissue broken down	Viable pollen	Sterile pollen
Flowers collected July 16, 1980				
9	1	+	x	x
	2	-		x
	3	+	x	
	4	+	x	
200	1	+	x	x
	2	+		x
	3	+		x
	4	+	x	x
229	1	+	x	x
	2	+		x
	3	+, -		x
	4	+, -	x	x
FD	1	+		x
	2	+	0	0
	3	-		x
Flowers collected May 20, 1981				
FD	1	+	x	
	2	+	x	
	3	+	x	
	4	+	x	
	5	+	x	

Appendix Table 3. Inflorescence type, flower buds, and subsequently developed fruit.

Genotype	Flower type	Flower opening	Buds per inflor.	Mature fruits per inflor.
9	scorpioid cyme	intermediate	3-4	1-3
110	" "	basipetally	3-6	1-3
200	racemose cyme	acropetally	5-8	3-5
229	" "	"	5-7	3-5
FD	" "	"	5-6	1-3

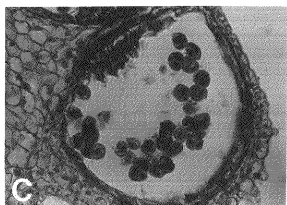
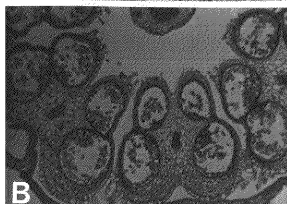
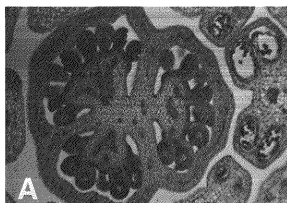
Appendix Fig. 1. Inflorescences bearing fruit. Scorpioid cyme: '9', '110'. Racemose cyme: '200', '229', 'FD'. Note that all inflorescences bear some vegetative blossoms.



Appendix Table 4. Temperatures affecting flower development and fruit set.

Flowers collected	Temps. ($^{\circ}\text{C}$) over 14 days before collecting flowers			
	Max.	Ave. max.	Lowest high	Range
May 1, 20, 1981	32.2	27.2		
July 16, 1980	37.8	36.9		
Fruits collected	Temps. ($^{\circ}\text{C}$) over 50 days before collecting fruits			
July 2, 1981	35.6	33.1	28.3	3 days at 35.6° and 5 days at 35°
July 17, 1980	38.9	37.1	33.3	50 days $>33^{\circ}$; last 31 days $>35^{\circ}$

Appendix Fig. 2. Flower in transverse sections. A. immature ovary.
B. immature anthers. C. anther locule containing
microspore tetrads.



VITA

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